PATTERNS OF EGG AND CLUTCH SIZE VARIATION IN THE MONTAGU'S HARRIER

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ABSTRACT.—We describe the phenotypic plasticity of egg and clutch size in the Montagu's Harrier (*Circus pygargus*) based on measurements of 1292 eggs from 403 nests and clutch sizes recorded at 579 nests in four study areas in western France and central Spain. Variability of egg size, clutch size and clutch volume was high (coefficients of variation 10, 24, and 28%, respectively). Egg volume and shape (length/width) were positively correlated and bigger eggs tended to be relatively longer. Shape was not normally distributed, with elongated eggs being more common than rounded ones. Montagu's Harriers appeared, therefore, to be less constrained to increase egg length than egg width. Egg volume was positively correlated with clutch size. The first and last eggs in each clutch were on average smaller than the intermediate ones, but the differences were not significant. High interannual variation existed in clutch size, but not in egg size. No regional variation was found in egg or clutch size, once interannual differences were taken into account. Overall, clutch size appeared to be a more plastic trait than egg size, although the large variability in the latter suggested that it had the potential, at least, to vary according to environmental or individual conditions.

KEY WORDS: *Montagu's Harrier*, Circus pygargus; *clutch size, egg size, phenotypic plasticity.*

Patrones de variación en el tamaño de puesta y de huevos en el Aguilucho Cenizo

RESUMEN.—Describimos la variabilidad fenotípica del tamaño de la puesta y los huevos en el Aguilucho Cenizo (*Circus pygargus*) basándonos en medidas de 1292 huevos procedentes de 403 nidos y en los tamaños de puesta observados en 579 nidos de 4 zonas de estudio localizadas en Francia occidental y España central. La variabilidad tanto del tamaño de los huevos como sobre todo del tamaño de puesta y del volumen de puesta fueron muy altas (con coeficientes de variación de 10, 24, y 28%, respectivamente). Se encontró una correlación positiva y significativa entre volumen y forma (longitud/anchura) de los huevos, es decir que los huevos más grandes tendían a ser proporcionalmente más alargados. La variable forma no estaba distribuida de manera normal; los huevos alargados eran más frequentes que los redondeados. Los Aguiluchos Cenizos parecen por tanto estar menos limitados para aumentar la longitud que la anchura de los huevos. Se encontró también una correlación positiva y significativa entre el volumen de los huevos y el tamaño de puesta. Los primeros y últimos huevos de cada puesta eran en general más pequeños que los intermedios, pero las diferencias no fueron significativas. Se encontraron diferencias interanuales significativas en el tamaño de puesta, pero no en el tamaño de huevos. En cambio, las diferencias entre las zonas de estudio no fueron significativas para ninguna de las dos variables. En general, el tamaño de puesta es un caracter mas flexible que el tamaño de los huevos, aunque la gran variabilidad en este último sugiere que tiene al menos el potencial de variar en relación a diversas características individuales o ambientales.

[Traducción Autores]

Among avian life history traits, egg size and clutch size have been traditionally considered as two major components of fitness (Stearns 1992).

These traits are direct measures of female investment in reproduction which have been shown to influence reproductive success in raptors (e.g.,

Hakkarainen and Korpimäki 1994, Wiebe and Bortolotti 1995). Understanding the patterns of egg and clutch size variation is, therefore, important in order to assess whether these traits are potentially adaptive. Montagu's Harrier (*Circus pygargus*) is a medium-sized palearctic raptor that breeds on the ground (Cramp and Simmons 1980), sometimes colonially (e.g., Cramp and Simmons 1980, Leroux 1987, Martelli 1987, Karpov and Berbaev 1990, Arroyo 1995). These characteristics facilitate sampling of a large number of nests, and indeed there are several studies reporting clutch sizes (Perez Chiscano and Fernandez Cruz 1971, Cormier 1985, Underhill-Day 1990, Pandolfi and Giacchini 1991, Martelli and Sandri 1991, Bijlsma et al. 1993, Krogulec and Leroux 1994). Even so, there are few multi-year studies, where among-year differences can be evaluated (Butet and Leroux 1993, Faralli 1994, Arroyo 1995, Castaño 1997), and fewer studies which report egg sizes (Studinka 1941, Schönwetter 1967, Hays 1971, Perez Chiscano and Fernandez Cruz 1971). The latter data, when given, refer just to unhatched eggs or are presented only as mean values. The general patterns and distribution of egg size variation have never been described for this species, nor has the relationship between egg size and clutch size. The aims of this paper are to describe the phenotypic plasticity of egg size in the Montagu's Harrier, its annual and geographical variability, and its relationship with clutch size. We show that egg size is highly variable, but that plasticity of egg volume is less than that of clutch size, with the latter showing a higher annual and regional variation.

METHODS

We systematically searched for nests in four study areas, which cover 200–300 km² each. Three of them were located in western France: Marais de Rochefort (45.57°N, 0 55°W, Charente-Maritime region), for which clutch size and egg size data were available from 1992–97; south of Deux Sèvres (46.11°N, 0.28°W, Poitou-Charente region), for which clutch- and egg-size data were available from 1994–97; and Baie de l'Aiguillon (46.24°N, 1.24°W, Département de la Vendée), with data collected from 1995–97. The fourth study area is northeast of Madrid, Spain (40.38°N, 3.30°W); clutch-size data from this area were collected since 1991 and egg-size data were available mainly for 1994, 1996 and 1997, although some scattered data existed from previous years.

Clutch size was known for 579 clutches. Additionally, 1292 eggs from 403 of these clutches were measured in the four study areas. Egg length and width were measured with a vernier calliper to the nearest 0.1 mm. From these two measurements, we derived two additional variables: egg volume, which was calculated from Hoyt's (1979) equation (volume (cm³) = 0.51 × length × width²/1000), and egg shape (length/width). To test for differences between measurers, 24 eggs in 1996 were measured by two different people. Measurements between observers were usually within 0.2 mm, and differences were rarely higher than 0.3 mm (<1% of average length or width). Slight, but significant differences were found in measurements of egg length (paired *t*-test, t_{24} = 2.30, P = 0.03). No significant differences were found for egg width measurements (paired *t*-test, t_{24} = 1.32, P = 0.20), or for egg volumes calculated from measurements from both observers (paired *t*-test, t_{24} = 1.00, P = 0.33). Thus, all data were pooled regardless of measurer.

Mean egg volume and clutch volume (sum of egg volumes in a clutch) were calculated for each clutch. In 47 clutches, measurements for some eggs were missing (either because one or two eggs had already hatched by the visit when egg measurements were taken, or because the nest failed after the first visit, when the clutch was incomplete). In those cases, clutch volume was calculated as mean egg volume (calculated from measured eggs) × clutch size (when final clutch size was known). Clutches of more than one egg in which only one egg was measured (N = 63) were excluded from clutch analysis.

Eggs were marked for identification with a (nontoxic) pencil when nests were visited. Egg rank was estimated for nests that were visited at least once during laying, according to shell color (eggs freshly laid being tinged blue, Balfour 1962), and degree of cleanliness (old eggs variably covered with earth, Simmons 1994). The relationship between egg rank and egg volume was analyzed for each clutch, grouping eggs in three egg categories (following Jover et al. 1993): first egg in the clutch, last egg in the clutch, and intermediate eggs (for which egg volume was averaged). Clutches where all eggs could not be assigned to one of these three categories were excluded for egg-rank analysis. Accuracy of ranking method was tested for 107 eggs from 50 nests that were visited during hatching, and proved to be higher than 94%.

Annual variation in mean egg size was calculated using clutch data from the four study areas for 1994–97 alone (as data for earlier years were not available or adequate for all study areas). Annual and regional variability in clutch size was analyzed with data from all nests visited, whether eggs were measured or not. All analyses were performed with SAS 6.11 statistical package.

RESULTS

The distributions of neither egg length, width or volume departed from normality (Table 1). Egg-shape, in contrast, differed significantly from a normal distribution (skewness = 0.67, Fig. 1), with long eggs being more frequent than round ones. Overall variation in egg length, as seen from the coefficient of variation, was slightly higher than that of egg width. The smallest egg was only 37.9% of the volume of the largest. Egg shape and egg volume were positively and significantly correlated

Table 1. Summary statistics for Montagu's Harrier eggs and clutches. N = sample size (number of eggs for egg biometrics, number of clutches for clutch size or clutch volume); SD = Standard Deviation; CV = Coefficient of variation, $100 \times SD/\bar{x}$; P = probability for departure from the normal distribution (Wilks-Saphiro test).

MEASUREMENT	N	MEAN	SD	RANGE	CV	P
Egg-length (mm)	1292	41.5	1.96	35.9–49.2	4.7	0.09
Egg-width (mm)	1292	33.1	1.22	27.0–39.1	3.7	0.20
Egg-volume (cm^3)	1292	23.2	2.36	13.3–35.2	10.2	0.98
Egg-shape	1292	1.25	0.06	1.05–1.52	4.8	0.0001
Clutch size	579	4.0	0.97	1–8	24.2	0.0001
Clutch volume (cm^3)	313	92.9	25.7	21.5–195.8	27.6	0.07

(r = 0.079, N = 1292, P = 0.004): larger eggs tended to be relatively more elongated.

A one-way ANOVA with all years and sites combined showed that 59% of the variance in mean egg volume was due to differences among clutches as opposed to differences within clutches ($F_{212,1002}$ = 6.82, P < 0.0001). Regarding within clutch variation, there was a tendency for the first and last eggs of a clutch to be smaller than the intermediate ones (Fig. 3), although differences were not significant (one-way ANOVA, $F_{2,376}$ = 0.7, P = 0.5).

Clutch size and clutch volume were more variable than egg size (see CV in Table 1). Most of the variability in clutch volume was due to clutch size (linear regression, $F_{1,311}$ = 2451, P = 0.0001, r^2 = 89%). Within each clutch size, the coefficient of variation of clutch volume was similar to that of egg volume (Table 2). After pooling all data, mean egg volume was significantly and positively correlated with clutch size (r = 0.157, N = 313, P = 0.005, Fig. 2). Thus, bigger clutches also had relatively larger eggs. Clutch size was also positively and significantly correlated with mean egg width (r =

0.152, N = 313, P = 0.006), but not with mean egg length (r = 0.110, N = 313, P = ns). Mean egg shape was not related to clutch size (r = −0.008, N = 313, P = ns).

We also pooled data from all years and compared the mean values for the different variables among the study areas (Table 3). A general linear model of clutch size in relation to site, year, and their interaction showed that clutch size varied significantly among years ($F_{3,561}$ = 13.7, P = 0.0001), and that there was a significant interaction between year and site ($F_{8,561}$ = 8.05, P = 0.0001). However, no significant differences among sites were found when year differences were taken into account ($F_{3,561}$ = 1.58, P = 0.2). Mean egg length, width, volume or shape did not vary significantly neither among sites nor among years (MANOVA, $F_{8,384}$ = 0.58, P = 0.79 for site effect; $F_{4,191}$ = 1.49, P = 0.21 for year effect, $F_{8,384}$ = 1.29, P = 0.25 for the interaction).
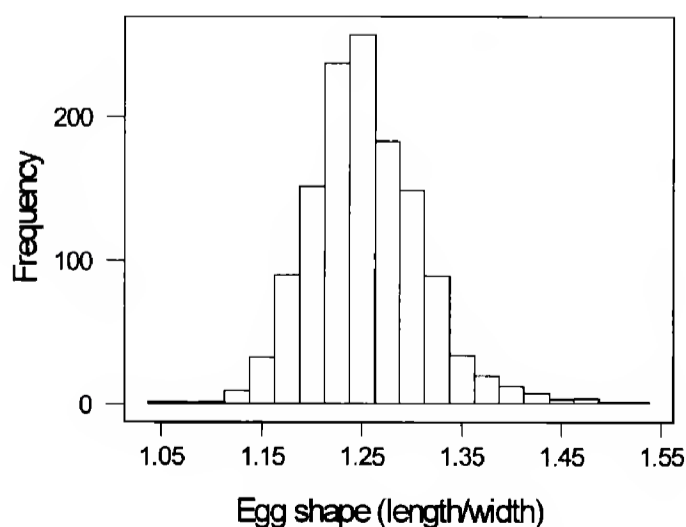

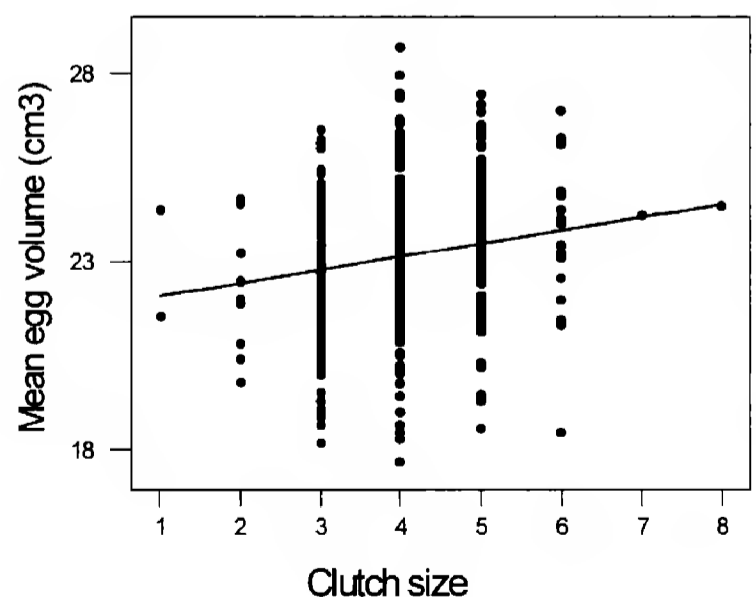Figure 1. Distribution of egg shapes (length/width) in the Montagu's Harrier.

Figure 2. Relationship between mean egg volume and clutch size in the Montagu's Harrier.

Table 2. Summary statistics of clutch volume in the Montagu's Harrier according to clutch size. N = sample size (number of clutches); SD = Standard Deviation; CV = Coefficient of variation, $100 \times SD/\bar{x}$.

Clutch Size	N	Mean	SD	CV
1	2	22.9	2.01	8.8
2	11	44.9	3.41	7.6
3	81	68.1	6.23	9.1
4	130	92.6	8.65	9.4
5	71	117.7	10.37	8.9
6	16	141.1	12.54	9.2
7	1	169.9	—	—
8	1	195.8	—	—

Discussion

Mean egg size values found in this study were similar to those reported in other studies (Studinka 1941, Schönwetter 1967, Hays 1971, Perez Chiscano and Fernandez Cruz 1971). Overall variability in egg size in the Montagu's Harrier was relatively high compared to that found for other nonpasserine species (Flint and Sedinger 1992, Swennen and van der Meer 1992, Jover et al. 1993, Meathrel et al. 1993, Hakkarainen and Korpimäki 1994, Robertson 1995, Weidinger 1996), but similar to that found in the American Kestrel (*Falco sparverius*) (Wiebe and Bortolotti 1995). Of the parameters contributing to egg volume, egg length was more variable than egg width, as seen from the coeffi-

cient of variation and the positive skewness of the distribution of egg shapes. Females augmented the volume of their eggs by increasing the lengths rather than the widths of their eggs, as reflected by the fact that egg volume and shape were positively correlated. This is opposite to what is reported for the American Kestrels (*Falco sparverius*), where the increase in egg volume was mainly the result of an increase in egg width (Wiebe and Bortolotti 1995). Similarly, in the Cape Petrel (*Daption capense*) the relationship between egg shape and volume was negative, with larger eggs being relatively more rounded (Weidinger 1996). As egg shape is determined during its passage through the oviduct (Campbell and Lack 1985), the reasons for these interspecific differences might be related to morphological, physiological or genetic differences between species.

Up to 59% of the variance in egg size was explained by differences among clutches, proportion similar to that of other nonpasserine species (see Wiebe and Bortolotti 1995 for a summary), but a lower figure than that reported for American Kestrels (Wiebe and Bortolotti 1995). Between clutch differences in egg size are related to differences between females, which are in turn linked to individual or environmental conditions. We found no significant effect of site or year on mean egg volume, although such effects have been found in other avian species (Flint and Sedinger 1992, Croxall et al. 1992, Robertson 1995, Weidinger 1996).
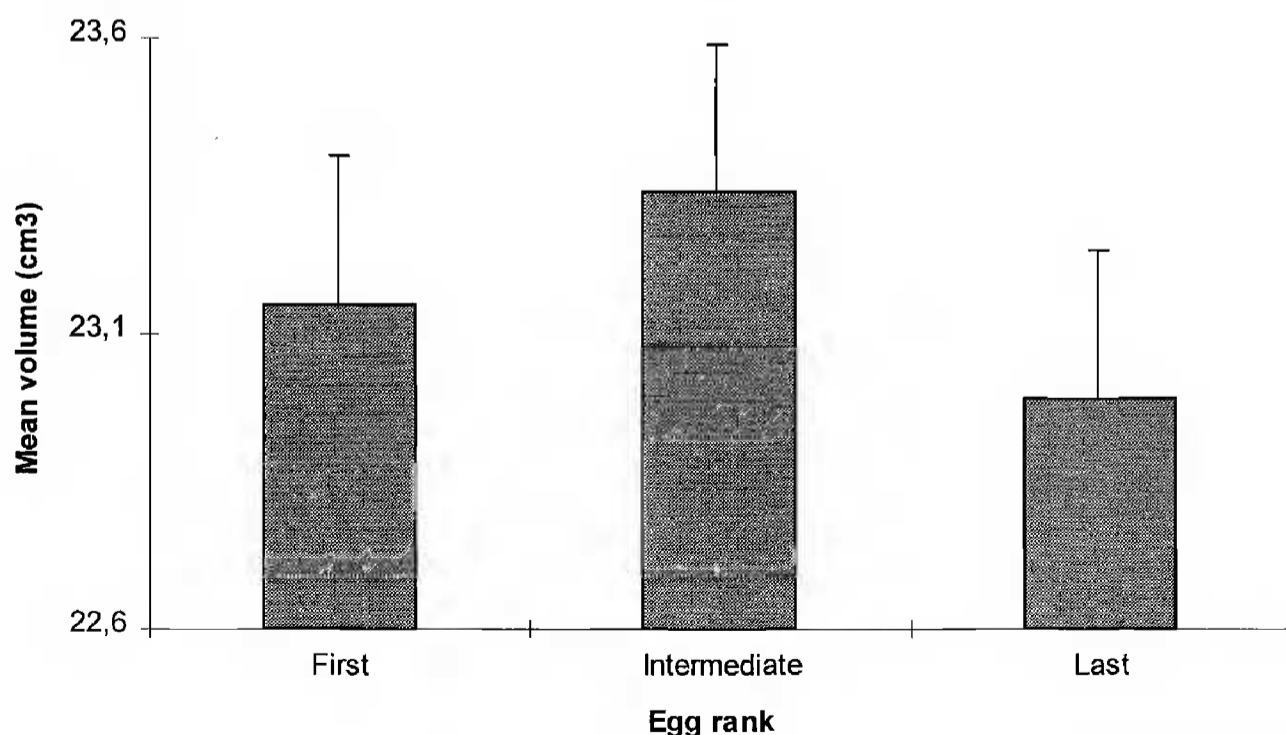

Figure 3. Mean (±SE) egg volume of first, intermediate and last eggs within clutches. Data from 92 clutches where rank order was determined. Volume of "Intermediate" eggs was averaged for each clutch.

Table 3.   Geographical differences in clutch parameters. Mean, SD, and sample size (number of clutches) in brackets.

	DEUX SÈVRES	ROCHEFORT	BAIE DE L'AIGUILLON	MADRID
Clutch size	4.28 ± 1.09 (143)	4.00 ± 1.04 (133)	3.75 ± 0.80 (101)	3.93 ± 0.84 (215)
Mean egg volume (cm³)	23.2 ± 2.16 (121)	23.3 ± 2.01 (107)	22.9 ± 1.95 (56)	23.0 ± 2.26 (42)
Mean egg length (mm)	41.6 ± 1.9 (121)	41.6 ± 1.6 (107)	41.1 ± 1.6 (56)	41.1 ± 1.6 (42)
Mean egg width (mm)	33.0 ± 1.0 (121)	33.1 ± 1.1 (107)	33.0 ± 1.0 (56)	33.1 ± 1.2 (42)

This might indicate that phenotypic plasticity in egg size according to environmental conditions is relatively limited in the Montagu's Harrier, maybe due to a high heritability or genetic component in egg size. Alternatively, the relationship between egg size and environmental conditions might be masked by more evident changes in clutch size, or modulated by changes in within clutch egg-size patterns, as has been shown for the African Marsh-Harrier (*Circus ranivorus*) (Simmons 1994). Within clutch differences in the Montagu's Harrier, which accounted for 41% of the variance in egg size, showed highly variable patterns, as was reflected by the large standard deviations in average egg sizes for each rank.

Variability in clutch size was higher in the Montagu's Harrier than in other species (Flint and Sedinger 1992, Wiebe and Bortolotti 1995), and much higher than that of egg size, indicating that clutch size was a trait with higher plasticity than egg size in this species. A higher variation in clutch rather than egg size according to food abundance was found in the American Kestrel (Wiebe and Bortolotti 1995). The higher flexibility of clutch size toward different environmental conditions was also reflected in the strong annual variation of this parameter. In contrast, no significant regional variation was found after annual differences were taken into account. Average clutch size in this study was similar or in the upper range to that reported in

Table 4.   Clutch size of Montagu's Harrier in different regions of its breeding range. $\bar{x}$ ± SD. N = sample size (number of nests). Regression of clutch size on latitude: $F_{1,17}$ = 1.91, P = 0.18, r^2 = 4.8%. When excluding one-year studies, $F_{1,14}$ = 0.50, P = 0.49, r^2 = 0%.

STUDY SITE	LATI-TUDE	CLUTCH SIZE	N	RANGE	LENGTH OF STUDY	REFERENCE
The Netherlands	53.30	4.20 ± 0.80	112	2–7	30	Bijlsma et al. 1993
Belarus	53.00	3.42	12	1–5	1	Yasevitch and Vintchewski, 1995
Poland	53.00	3.90–4.40	125	2–5	several	Krogulec and Leroux 1994
England	52.30	4.02 ± 0.07	227	2–10	30	Underhill-Day 1990
Morbihan, France	47.44	4.27 ± 0.14	29	3–6	14	Hays 1971
Milly, France	47.10	3.69 ± 0.19	26	2–5	>4	Cormier 1985
Noirmoutier, France	47.01	3.61 ± 0.17	23	2–5	>4	Cormier 1985
Rochefort, France	45.57	2.80 ± 0.40 – 4.05 ± 0.18	162		7	Butet and Leroux 1993
Rochefort, France	45.57	4.00 ± 1.04	133	1–6	6	This study
Deux Sèvres, France	46.11	4.28 ± 1.09	143	2–8	4	This study
B. Aiguillon, France	46.24	3.75 ± 0.80	101	2–6	3	This study
N. Apennines, Italy	43.28	3.32	31		5	Faralli 1994
Marche, Italy	43.40	3.80	37		2	Pandolfi and Giacchini 1991
Emilia-Romagna, Italy	44.30	3.70 ± 0.80	61	2–5	7	Martelli and Sandri 1991
Madrid, Spain	40.38	3.93 ± 0.84	215	2–6	6	This study
Ciudad Real, Spain	38.35	4.30 ± 1.00	120	2–9	7	Castaño 1997
Madrigalejo, Spain	39.09	3.48 ± 0.99	98	1–5	5	Corbacho et al. 1997
Cáceres, Spain	39.25	3.31 ± 0.65	19	2–5	1	P. Chiscano and F. Cruz 1971
Castro Verde, Portugal	37.42	2.82 ± 0.40	11	2–3	1	Onofre 1992

other areas (Table 4). It has been reported that clutch size in this species increases with latitude (Corbacho et al. 1997). However, our wider analyses show that the relationship is not significant, especially if only the studies with data of at least two yr are considered given the potential annual variation of this parameter. This indicates that the pattern is more complex than just latitudinal, and probably more related to the the relative food abundance between regions, or to the relative variation in food abundance among years within each site.

Life-history theory predicts a trade-off between the number and size of offspring produced (Stearns 1992). Thus, a negative relationship between clutch and egg size is generally expected (Blackburn 1991), and has been found in some species (Potti 1993, Rowe 1994). In the case of the Montagu's Harrier, this relationship was positive, which suggests that this particular trade-off does not exist in this species. Actually, no relationship between clutch and egg size has been found in some species (e.g., Duncan 1986, Järvinen 1991, Hakkarainen and Korpimäki 1994), while others show, as the Montagu's Harrier, a positive relationship (Flint and Sedinger 1992). In the American Kestrel, mean egg volume increases with increasing clutch size, except for the largest clutches where it declines (Wiebe and Bortolotti 1995). However, a trade-off will only be evident for a given amount of resources. The positive relationship between clutch and egg size might simply come as a result of pooling years and sites where the available resources are very different.

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